

# CYTOLOGICAL STUDIES OF SOME OF THE SHORT-CYCLED RUSTS

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## INTRODUCTION

Poirault and Raciborski (13) in 1895 and Sappin-Trouffy (14) in 1896 were among the first authors to give definite information concerning the condition of the nuclei in the Uredinales. As a result of their investigations, it was found that the young teleutospore is binucleate but that before maturity the nuclei fuse. Upon germination of the teleutospore a four-celled basidium is formed, each cell of which produces a uninucleate basidiospore. Previous to spore formation, the fusion nucleus of the promycelium undergoes meiosis. The mycelium arising from these spores remains uninucleate until just before formation of the aecidiospore. From this mycelium a second type of spore, the spermatium, may be formed. According to Sappin-Trouffy, the binucleate condition arises by a nuclear division which is not followed by a cell division. It was soon found, however, that such a condition does not occur in all rusts.

Blackman and Fraser (3), making a careful study of *Puccinia malvacearum* Mont., a lepto-form, found that the uninucleate vegetative mycelium gives rise to a sorus with binucleate hyphae. From special cells of these hyphae the teleutospores originate. Cases were noted by them in which the hyphae and teleutospores are trinucleate. They are unable to conclude just how this change from the uninucleate to the bi- or trinucleate condition was brought about. In *Puccinia poarum* Niels., a heteroecious form, they find nuclear migrations in the aecidium and trinucleate teleutospores in the mature teleutosorus. From the similarity of trinucleate teleutospores in *Puccinia malvacearum* and *Puccinia poarum*, they conclude that the method by which the binucleate condition is brought about in the aecidium and in the young teleutosorus may be similar. In

micro forms, *Puccinia adoxae* D. C. and *Uromyces scillarum* Wint., they find that both the vegetative mycelium and the young teleutosori are binucleate. In a third form, *Uromyces ficariae* Lev., the mycelium appears to be predominantly uninucleate, with the exception of that at the base of the teleutosorus, which is binucleate. The origin of this binucleate condition is assumed to be similar to that of *Puccinia malvacearum*, i. e., by nuclear migrations or cell fusions between cells at the base of the young teleutosorus in the case of *Uromyces ficariae*, and between the vegetative cells at some time early in the life history of the mycelium in *Puccinia adoxae* and *Uromyces scillarum*.

Olive (11) in studying the micro form *Puccinia transformans*, discovers that the binucleate condition is brought about by the absorption of the walls of two adjacent cells which are in contact. These cells were either in a vertical or a horizontal position. From these fusion cells the teleutospores develop. In a later paper Olive (12) states that there are two types of short-cycled rusts with reference to the time at which the binucleate condition is brought about. In one type, the binucleate condition originates at the base of the young teleutosorus, examples of this being *Puccinia elegans* Schroet., *P. asteris* Schw., and *P. malvacearum* Mont.; in a second type the binucleate condition originates at some indefinite point earlier in the life history of the vegetative mycelium. Except in one species, *Puccinia elegans*, in which the sexual fusions have been studied, the method of the initiation of the binucleate condition is problematical. *Uromyces rudbeckiae* Arth. and Holw. is an exception to the preceding forms in as much as all of the cells of the mycelium are uninucleate. Werth and Ludwigs (16), in 1912, working on *Puccinia malvacearum*, found, however, that cell fusions occur between uninucleate cells of unequal size and that the nucleus of the smaller migrates to the larger cell.

Kursanov (8) finds that *Uromyces laevis* Körnicke is characterized by a uninucleate vegetative mycelium which becomes binucleate at the base of the sorus. Both teleutosori and spermogones were borne on the lower surface of the leaf. *Puccinia ficariae*, which had been previously examined by Sappin-Trouffy (14) in 1896, Blackman (2) in

1906, and Moreau (10) in 1914 was found by Kursanov to be characterized by a mycelium predominately binucleate. Examination of *P. asarina* by Kursanov showed that early in its life history the mycelium was uninucleate but later binucleate. The entire mycelium of two other short-cycled forms, *Puccinia fergussonii* B. and Br., and *Uromyces gageae* Beck., appeared to be binucleate. Spermogones are not developed.

Further study of *Puccinia malvacearum* by Lindfors (9) showed that cell fusions occurred early between cells of young teleutosorus, and that often the binucleate cells are separated by sterile cells. Similarly cell fusions were found by Lindfors in *Tranzschelia fusca* (Pers.) Diet. However, if the cells are in contact with each other, nuclear migrations occur through a small pore. *Puccinia morthieri* Koern., which had previously been described by Fischer as having a uninucleate mycelium, was found by Lindfors to have binucleate cells, which arise by cell fusions. The results of his study on *Chrysomyxa abietis* (Wallr.) Ung. are identical with those of Kursanov, the binucleate condition resulting from the absorption of the cell wall between two adjacent cells.

In *Puccinia arenariae* (Schum.) Wint., cell fusions did not occur in the sorus, the mycelium being already binucleate. A study of germinating teleutospores showed that the fusion nucleus undergoes two divisions which are followed by only one cell division, thus forming a two-celled binucleate basidium. Supposedly two nuclei enter each basidiospore, and the mycelium resulting is binucleate. *Puccinia albulensis* Magn., *P. epilobii* DC., *P. gigantea* Karst., *P. holboelli* Hornem., *P. saxifragae* Schlecht., and *Uromyces solidaginis* (Sommerf.) Nieszl. show binucleate "vegetative mycelium" before sorus formation, which means that this condition must have developed early. Just how it came about is problematical. In *Puccinia epilobii* three nuclei are often found in the cell which is to form the teleutospore.

Cell fusions have also been described by Dodge (7) for *Gallowaya pinicola* Arth. These fusions appear to occur readily between the second or third cell from the outer end of the chains, just after the epidermis is ruptured.

From the literature one can see that the short-cycled rusts are characterized by a uni- or binucleate vegetative mycelium which gives rise to the binucleate teleutospore. Studies were made of *Puccinia asteris* Schw., *P. cryptotaeniae* Peck., *P. xanthii* Schw., *P. waldsteiniae* M. A. Curt., and *P. fusca* (Pers.) Relh. by the author, with the end in view of determining in each case whether the mycelium is uninucleate or binucleate, and if binucleate, how this condition arises.

#### MATERIAL AND METHODS

The material for these studies was collected by Professor E. M. Gilbert and Dr. J. J. Davis in various localities in northern Wisconsin in the seasons of 1921 to 1925 inclusive. Flemmings' medium and alcohol formal acetic solutions were used for fixation. Sections were cut from 3 to 25 $\mu$  thick and stained with Flemming's triple stain or with Heidenhain's iron-alum haematoxylin, with counter stains of erythrosin, light green, and orange G. Iron-alum haematoxylin with erythrosin gave the best results.

#### OBSERVATIONS

##### *Puccinia asteris* Schw.

Material of *Puccinia asteris*, a micro-form growing on *Asteris macrophyllus*, showed that the mycelium is made up of cells varying in size and in the number of nuclei. The vegetative mycelium is much branched and not only ramifies throughout the intercellular spaces of the leaf, but also penetrates the cells of the leaf (Pl. 8, fig. 2), forming on the under surface a large, broad, flat sorus with no peridium.

Olive (11), working on *Puccinia asteris*, found that the binucleate condition arises at the base of the sorus. In very young material, from which the present study was made, hyphae with long binucleate cells were found in the intercellular spaces of the leaf some distance from the sorus (fig. 1). Associated with these binucleate cells are short uninucleate cells with large elongated nuclei and dense cytoplasm (fig. 4). Smaller binucleate cells with their nuclei about half the size of those of the uninucleate

cells are also visible in the intercellular spaces (fig. 3). It seems probable that the smaller nuclei may have resulted from the division of the larger nuclei without being followed by cell division. In addition, uninucleate cells, about half the size of the binucleate cells, are also present (fig. 6). This would seem to indicate that in such a case cell division has followed nuclear division. Instances were observed in which the nuclei of the binucleate cells were undergoing nuclear division (fig. 9), and if this is followed by cell division, the daughter cells will be binucleate.

The cells at the base of the sorus are shorter and wider than those found in the intercellular spaces. No cell fusions were seen to occur between the cells at the base of the sorus, the cells being already binucleate. By nuclear and cell division these cells form the binucleate basal cells, which in turn by a series of nuclear and cell divisions give rise to the teleutospores. In mature sori three-, four-, and five-nucleate cells were not infrequently observed among the cells at the base of the sorus (figs. 7, 8) which in this instance seems to indicate that nuclear division is not always followed by cell division. This irregularity makes it seem more probable that the binucleate condition may arise in a vegetative manner as claimed by Dodge and Kursanov. Dodge (6) found in a preparation of a uninucleate aecidial sorus of *Caecoma nitens* on blackberry, that chains of two nucleate spores and interstitial cells are adjacent to chains of uninucleate spores (Pl. 2, D). Cell fusions are not present in the sorus. He believes that it is not impossible that the binucleate spore arose by nuclear division. Kursanov (8) reports a similar condition for *Aecidium leucospermum*. His opinion is that the nucleus of the original basal cell simply divides and that a succession of binucleate cells are cut off.

#### *Puccinia cryptotaeniae* Peck.

Sections of leaves of *Cryptotaenia* sp. infected with *Puccinia cryptotaeniae* upon examination show that there is little branching of the mycelium previous to the formation of the teleutosorus which differentiates very early. The hyphae push out between the spongy cells directly below

the epidermis, forming a compact mass, the young teleutosorus. With the growth of the hyphae, the epidermis is stretched, pushed out, and ruptured. Soon after the epidermis is ruptured, the hyphae at the periphery of the sorus branch profusely, forming a peridial-like layer composed of uninucleate cells (Pl. 2, fig. 21). At maturity the sorus is cup-shaped and is imbedded in the leaf, due to the formation of the sorus primordium deep within the leaf. In some instances the sorus appears to extend almost through the entire leaf. The teleutosori may occur on either side of the leaf and may be found in all stages of development.

Very early in the development of the young sorus, even before the epidermis is ruptured, the mycelium is both uni- and binucleate. The binucleate condition can be accounted for in part by the fact that the binucleate hyphae of the young sorus can be traced to a nearby mature sorus. Nuclear migrations between two adjacent cells at the base of the sorus (fig. 18) as described by Blackman (2) for *Phragmidium violaceum* are rare. Peculiar cell fusions are found in which the lower portion of the cell walls of two erect adjacent cells are partially absorbed (figs. 17, 19). Since these seem to have arisen from binucleate basal cells, the significance of such fusions is unknown. From my observations the cells of the hyphae forming the peridium remain uninucleate by means of nuclear and cell divisions.

Examination of cross sections of petioles show that there is an abundance of vegetative hyphae. These branch abundantly and vary in respect to the size of the cells and number of nuclei. Some of the cells contain a single nucleus, others two nuclei. In still other cells nuclei may be found in the process of division. The mycelium branches profusely through the intercellular spaces of the petiole, forming more or less of a network. When an apical cell of a hypha comes in contact with a host cell a short terminal uninucleate cell, the haustorium, is formed by nuclear and cell division. This cell, after penetrating the host cell, increases in size and becomes ovoid in shape. From my observations the haustoria are always uninucleate, although both uninucleate and binucleate vegetative hyphae are present (fig. 22). As the vegetative mycelium is apparently

uninucleate in the beginning, it is to be expected that the haustoria would be uninucleate rather than binucleate as described by Allen (1) and by Smith (15).

Numerous sori are found, some being formed internally in the large intercellular spaces of the petiole. The nuclei of uninucleate cells which are about to undergo division take up a central position in the cell. The nuclear membrane disappears and the chromatin material may at times become an irregular deeply-staining mass (fig. 14). More often the chromatin assumes a dumb-bell shape (fig. 12), which pulls out eventually into two pear-shaped bodies forming the two nuclei. In adjacent cells there are nuclei which, according to their size, would lead one to conclude that they are the daughter nuclei of a recent nuclear division (fig. 13).

Conjugate division also frequently occurs, followed by cell division. Just previous to conjugate division the nuclei line up side by side at right angles to the long axis of the cell. Following cell division the nuclei migrate to a more central position in each daughter cell, usually lying parallel to the long axis of the cell, and remain thus until ready to undergo division again (fig. 15). Flask-shaped spermogonia are rare and occur on the lower surface of the leaf.

#### *Puccinia xanthii* Schw.

Very young material of this species was found growing on *Xanthii* sp. In sections of leaves showing young sori, the uninucleate hyphae grow parallel to the palisade cells near a stomatal opening (Pl. 3, fig. 23). Even before the epidermis is ruptured binucleate cells arise by an absorption of the walls of two adjacent uninucleate cells (fig. 23). The fusing cells are not regularly in rows, although in most instances observed they are the terminal cells of the hyphae. With the disappearance of the walls of the adjacent cells the nuclei take up a central position. They are characterized by a well marked nucleolus and chromatin network. The latter is not visible unless very densely stained. The cell enlarges and the nuclei prepare for division. With the disappearance of the nuclear membranes, the chromatin of each nucleus assumes a dumb-bell shape which pulls out

into two pear-like bodies. Cell division follows. These binucleate cells which are cut off from the basal cells may act as buffer cells against the epidermis (fig. 24). The cytoplasm of the buffer cells becomes vacuolate and the nuclei soon disintegrate. With the growth of the basal cells followed by the formation of other binucleate cells, the buffer effect is increased, and the epidermis is finally ruptured. It is not improbable that single uninucleate cells may act as buffers before cell fusions occur, although in the material from which the present study was made not a single instance of such a cell was observed. At maturity the sori are broad and flat. Trinucleate cells are very frequently visible (fig. 25). Since triple cell fusions are not found, it seems logical to assume that in such a case this trinucleate condition arises in a vegetative manner *i. e.*, by nuclear divisions which are not followed by cell divisions, as previously described for *Puccinia asteris*. The nuclei of these trinucleate cells undergo division (fig. 26) by pulling out into six pear-shaped masses similar to those found in the cells which are to form the teleutospores of *Puccinia fusca*.

*Puccinia fusca* (Pers.) Relb.

The material of *Puccinia fusca* on *Anenome* sp. showed all stages of development, from distinctly uninucleate vegetative mycelium to fully-formed binucleate teleutospores. The mycelium is much branched, and is both inter- and intra-cellular. In sections of leaves showing young sori, the hyphae are in regular rows at right angles to the epidermis, forming a compact mass beneath the epidermis. These may occur on either side of the leaf, although they are usually found on the lower surface of the leaf. The cells of the intercellular vegetative hyphae are long and possess a single elongated nucleus with chromatin network, nucleole, and nuclear membrane. These are often seen in preparation for division with the nucleoli lying free in the cytoplasm (fig. 29). The cells at the base of the sorus are shorter and thicker than those found in the intercellular spaces and at first contain a single spherical nucleus with one or more nucleoli. Later the nucleus becomes ovoid in shape and the chromatin condenses to one side of the nu-



cleus, usually opposite that of the nucleolus (fig. 34). With the disappearance of the nuclear membrane the nucleolus comes to lie free in the cytoplasm (fig. 31). The chromatin material undergoes division, forming the binucleate basal cell (fig. 33). Occasionally cell fusions occur in which the wall between adjacent cells disappears (fig. 32) such as described by Lindfors (9; Taf. III, fig. 24). This change from a uninucleate to a binucleate condition takes place at several different points in the sorus and not once for all, as is indicated by the fact that the hyphae of the middle of the sorus are more mature than those toward the periphery.

From these binucleate basal cells teleutospores develop. The young teleutospore appears first as an elongated binucleate cylindrical outgrowth from the basal cell (fig. 27). The paired nuclei soon undergo two divisions, the first division cutting off a stalk cell and a terminal cell. In the second division the upper cell divides to form the two cells of the teleutospore. The stalk cell becomes very long and large vacuoles appear at both ends of the cell. The nuclei are left imbedded in a dense mass of cytoplasm which gives the cells a plasmolyzed appearance (fig. 28). Occasionally the basal cell may produce a second cell between itself and the stalk cell (fig. 30). From my observations, these cells did not develop further. Accompanying the growth of the stalk cell, the two cells of the teleutospore increase in size, become more globular, especially the upper one, and the walls thicken irregularly with large wart-like projections. Spermogonia were found on the under surface of the leaf. They are typical flask-shaped structures and appear to originate from uninucleate mycelial cells similar to those which give rise to the uninucleate basal cells. From these cells arise the hyphae which by nuclear and cell division form the spermatia. At maturity, the spermatia are small, uninucleate cells, with a large, dense nucleus and a very small amount of cytoplasm.

#### Nuclear Phenomena in *Puccinia fusca* (Pers.) Relh.

The two nuclei of the cell which is to form the teleutospore are seen lying side by side parallel to the long axis of the cell (fig. 35). The nuclei are completely organized with membrane, chromatin net-work and nucleolus. The

chromatin resembles a coarse network, and at this stage it is very dense and appears to have accumulated at one side of the nucleus opposite the nucleolus (fig. 36). As the nuclear membranes disappear near the nucleoli, the nucleoli are left free in the cytoplasm. As development proceeds, the chromatin masses become irregular and roughly star-shaped (fig. 37), similar to those described by Blackman for *Phragmidium violaceum*. In preparation for nuclear division the chromatin nearest the basal portion of the cell takes a position near the second chromatin mass which occupies a more or less central position in the cell (fig. 38). In the meantime the nucleoli have migrated into the cytoplasm at some distance from the chromatin masses.

Olive (11) in his researches on *Triphragmium ulmariae* finds that the process of nuclear division is essentially the same in all types of cells, binucleate or uninucleate, being a mitotic process. Each nucleus during conjugate division acts entirely independent of its associated nucleus. Nuclear division occurs by the "aid of a centrosome" which is located on the nuclear membrane and which in some forms persists in the resting stages as a distinct "point of polarization" of the nuclear content. Soon the nuclear membrane breaks down, and the central spindle becomes a strongly developed structure apparently of dense filamentous nature which stretches between the two diverging centrosomes. In conjugate division the two spindles remain separate and distinct. Lindfors (9), in his studies on *Melampsora reticula*, also finds that a spindle is formed between two darkly-stained centrosomes which were not seen before nuclear division and which are unusually small. The spindle represents a dense homogenous cytoplasmic structure in which no fibers are present. From my observations of the material of this study, neither centrosomes are present nor is a definite well-organized spindle visible. The chromatin elongates into two dumb-bell-shaped masses which pull out into pear-shaped bodies as they approach the poles (figs. 39, 40, 41). As these bodies become further and further apart, the threads connecting them become indistinguishable in the cytoplasm. These thread-like fibers might be considered a rudimentary spindle. The pear-shaped bodies remain as distinct units, two to each end of the cell. Figure

43 shows an instance where three nuclei have divided, and three pear-shaped masses are present at each end of the cell. It was the appearance of a similar pear-like chromatin mass which led Poriault and Raciborski (13) to believe that such a chromatin mass represented a single chromosome, while Sappin-Trouffy (14), observing two such masses, concluded that the nuclei in Uredineae possess two chromosomes. Blackman (2), however, in studying nuclear division in the promycelium of *Gymnosporangium clavariaeforme* found that there are at least ten chromatin masses which he called chromosomes. These are aggregated into two distinct chromatin groups as they begin to migrate towards the poles. Olive (11) reports eight chromosomes for *Triphragmium ulmariae*. Lindfors (9) also reports eight for *Puccinia arenariae* and Colley (5) reports a possible eight for *Cronartium ribicola*. From my observations it seems hardly probable that these bodies as shown in figures 41 and 43 are chromosomes but rather that they are undifferentiated chromatin masses. After reaching the poles these pear-like bodies assume the typical spherical shape of the nuclei (fig. 42). The "cast out" nucleoli, which have persisted in the cytoplasm up to this time, slowly becoming less dense and often decreasing in size, finally disappear. The cytoplasm assumes a more vacuolate character, with the exception of that remaining in the equatorial region of the cell. Cell division follows and the nuclei which have been in opposite ends of cells take up a more central position in each of the cells. These are very dense and contain a single nucleolus. With the growth and maturity of the teleutospore the two nuclei of each cell come to lie close together, the nuclear membranes disappear and the two daughter nuclei reorganize into the fusion nucleus of the maturing teleutospore.

#### DISCUSSION

From the results of Kursanov (8), Lindfors (9), Dodge (6 and 7), and others, and from the foregoing results it can be seen that the binucleate condition of the short-cycled rusts may arise in a variety of ways and in a different manner in the same species. According to H. S. Jackson, in an unpublished paper, this may be entirely possible. He

believes that the short-cycled rusts have probably not all originated in one manner. A large majority of the micro-forms of *Puccinia* and *Uromyces* may have been derived directly from the aecidium of heteroecious eu species. One would expect to find in such forms a uninucleate primordium, which would produce teleutospores instead of aecidiospores. Of the forms studied above, *Puccinia cryptotaeniae*, with its aecidial-like sorus and its binucleate condition arising by nuclear migration and cell fusion, might possibly be an example of this type.

If, however, a short-cycled rust has not been recently derived from the aecidium, then it may have lost the aecidial-like characters. *Puccinia asteris*, with its large sorus and binucleate mycelium arising in a vegetative manner, seems to be characteristic of such a type.

Other micro-forms may have been derived from autoecious species not directly from the aecidium, but rather by passing first into a brachy-form and finally into a micro-form. Such species would be characterized by a flat, open type of sorus and with binucleate mycelium. Still other micro forms may be derived from an autoecious species in a manner similar to those which have been derived from a heteroecious eu species. Although Professor Jackson believes that the above conditions are probably so, exceptions show, however, that no general conclusions can be drawn and that the binucleate condition does not arise in any one fixed manner.

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#### SUMMARY

Young hyphae of *Puccinia asteris* show both uni- and binucleate cells, the nuclei of the latter being about half the size of the nuclei of the uninucleate cells. Conjugate division also occurs. Three-, four-, and five-nucleate cells were not infrequent. As no cell fusions were observed, it seems probable that the binucleate condition is brought about in a vegetative manner, that is, by simple mitotic division without being followed by cell division. Spermatogonia are not formed.

The binucleate condition of *Puccinia cryptotaeniae* arises at the base of the sorus and in the vegetative mycelium by nuclear division without a subsequent cell division and rarely by nuclear migration. Conjugate division frequently occurs in the vegetative mycelium. Flask-shaped spermogonia are rarely present.

Material of *Puccinia xanthii* shows that nuclear fusions occur very early in the formation of the teleutosorus, usually between terminal cells of adjacent hyphae. Binucleate basal cells cut off binucleate buffer cells which aid in rupturing the epidermis. Trinucleate cells are visible and since triple cell fusions were not observed, it is probable that this condition arose in a vegetative manner. Spermogonia are not present.

The vegetative mycelium of *Puccinia fusca* is uninucleate, becoming binucleate at the base of the sorus by cell fusion and by nuclear division without being followed by cell division. In both simple and conjugate nuclear division the chromatin mass pulls out into pear-shaped bodies which, upon reaching the poles, reorganize into daughter nuclei. Neither centrosomes nor a well-organized spindle are present. Flask-shaped spermogonia are formed.

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EXPLANATION OF PLATES

All figures were drawn with a camera lucida and with a Leitz 4-ocular and 1/16 oil immersion, making a magnification of 1850.

PLATE 8

- Figs. 1-9, *Puccinia asteris*; Fig. 10, *P. cryptotaeniae*.  
Fig. 1. Binucleate cell of vegetative mycelium.  
Fig. 2. Host cell after penetration of the haustorium.  
Fig. 3. Binucleate cell of the vegetative mycelium.  
Fig. 4. Uninucleate cell previous to nuclear division.  
Fig. 5. Binucleate cell at the base of the teleutosorus.  
Fig. 6. Uninucleate cell of the vegetative mycelium.  
Fig. 7. Five-nucleate cell of the vegetative mycelium.  
Fig. 8. Four-nucleate cell of the vegetative mycelium.  
Fig. 9. Conjugate division.  
Fig. 10. Longitudinal section of young teleutosorus showing nuclear division and cell fusion.

PLATE 9

*P. cryptotaeniae*.

- Fig. 11. Branching hyphae in the intercellular spaces of the petiole.  
Fig. 12. Single nucleus dividing.  
Fig. 13. Daughter nuclei of a recent division.  
Fig. 14. Chromatin in an irregular mass previous to nuclear division.  
Fig. 15. Nuclei assuming a position at right angles to the long axis of the hypha in preparation for conjugate division.  
Fig. 16. Conjugate division.  
Fig. 17. Peculiar cell fusion between terminal cells of two hyphae which appear to have arisen from binucleate basal cell.  
Fig. 18. Basal cells showing nuclear migration.  
Fig. 19. Cell fusion.  
Fig. 20. Nuclear division.  
Fig. 21. Branching hyphae forming the peridium.  
Fig. 22. Host cell with haustorium.

PLATE 10

- Figs. 23-26, *P. xanthii*; Figs. 27-44, *P. fusca*.  
Fig. 23. Longitudinal section of young sorus showing cell fusion.  
Fig. 24. Portion of young sorus with disintegrating buffer cells.  
Fig. 25. Hyphae with bi- and trinucleate cells.  
Fig. 26. Trinucleate division.  
Fig. 27. Basal cell with binucleate outgrowth.

Fig. 28. Stalk cell with terminal cell which will develop into teleutospore.

Fig. 29. Uninucleate cell of vegetative mycelium. Nucleole lying free in cytoplasm.

Fig. 30. Teleutospore with a second cell between stalk and basal cell.

Fig. 31. Uninucleate basal cell with nucleole lying free in the cytoplasm.

Fig. 32. Cell fusion of two adjacent hyphae.

Fig. 33. Uninucleate cell previous to nuclear division. After nuclear division.

Fig. 34. Nucleole of uninucleate basal cell being "cast into the cytoplasm".

Fig. 35. Binucleate cell with nuclei in a resting condition.

Fig. 36. Binucleate cell with nucleoles being extruded into the cytoplasm.

Fig. 37. Chromatin material lying free in the cytoplasm. One nucleole visible.

Fig. 38. Chromatin material in position previous to nuclear division.

Fig. 39. Rod-like masses of chromatin with nucleoles.

Fig. 40. Chromatin material pulling out into pear-shaped masses.

Fig. 41. Chromatin after pear-like bodies have reached the poles.

Fig. 42. Daughter nuclei in resting condition.

Fig. 43. Cell in which three nuclei have pulled out into pear-like chromatin bodies at each pole.

Fig. 44. Cell fusion.













